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A NUTRITIONAL EXPLANATION FOR BODY-SIZE PATTERNS OF RUMINANT AND NONRUMINANT HERBIVORES

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A number of researchers have discussed the importance of the relationship of metabolism and gut capacity to body size to explain diet composition in animals that consume primarily plant material (Short 1963; Prins and Geelen 1971; Janis 1976; Parra 1978; Hanley 1980; Demment 1983). The kinetics of food-particle passage in the gut determines the digestibility of the diet and is dependent upon gut volume and food intake (Van Soest 1982). Gut volume is a constant proportion of body weight (Parra 1978; Demment 1982), while maintenance metabolism (a prime determinant of intake) is a fractional power of body weight (Kleiber 1975). Since these two factors influence retention times of food particles and hence affect the extent of digestion of the diet, body size has been considered as a possible mechanism for interspecific differences in diet (Bell 1970; Hanley and Hanley 1980; Sinclair 1977; Demment 1980; Van Soest 1982).

In this paper, the relationship between body size and digestive capacity is used in conjunction with the relationship between abundance and quality of plant food to discuss the relative efficiencies of ruminant and nonruminant digestion at different body sizes. The relative efficiencies of digestion are used as a basis to explain the number of species of ruminant and nonruminant herbivores relative to body weight. While arguments are presented about physiological constraints on extant animal species, the principles discussed are considered as factors that have shaped the evolution of body size in these groups.

BODY SIZE AND DIGESTIVE CAPACITY

Because basal metabolic rate (kcal/kg/day) decreases nonlinearly with body weight, the total metabolic requirement of mammalian herbivores, MR (kcal/day), increases as

$$MR = 70\ W^{.75} \tag{1}$$

(Kleiber 1975) where W is weight in kg. The exponent .75 is used because the problems considered in this paper deal largely with interspecific comparison

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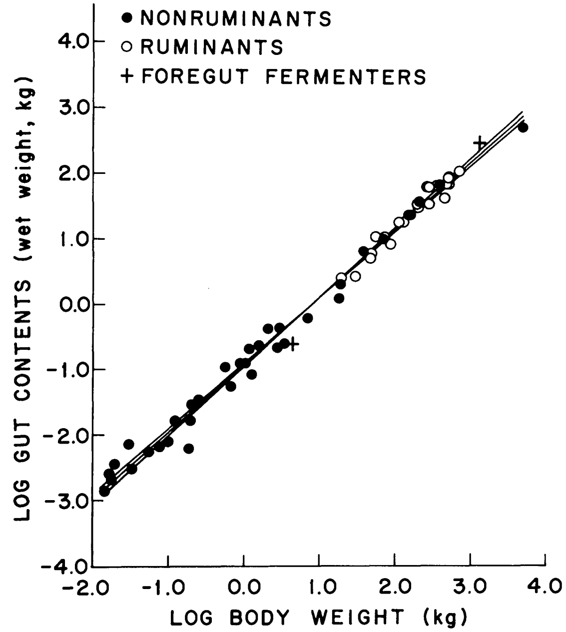

FIG. 1.—Log of gut contents is regressed against body weight for herbivores. Regression equation for all herbivores is $\log y = 1.032 \log x - .936$, $r = .99$, $n = 59$. Regression equations for ruminants and nonruminants were determined separately and were not significantly different in slope ($F = 1.745$; $V_1 = 1$, $V_2 = 53$; $P = .38$). The confidence intervals (± 5%) of the slope are indicated.

across a wide range of body sizes. Intraspecific regressions often yield exponents for this relationship quite different from .75 (Thonney et al. 1976). Weight and age are correlated and older animals have a greater proportion of their weight in fat. Since fat requires less maintenance energy than the equivalent muscle weight, the slope of the metabolism-to-body-weight curve is often less than .75. These lower exponents within species will accentuate the *MR/GC* (metabolic requirement to gut-capacity ratio) effect discussed below. Because *MR* increases with weight at a decreasing rate, large animals always require more total energy, but small animals require more energy relative to their body weight.

The capacity of the gut determines, in part, the capacity for digestion in an herbivore. Parra (1978) plotted the wet weight of gut contents of both ruminant and nonruminant herbivores against body weight. Additional data on this relationship, especially in the very large and small body sizes, have been collected (Demment, unpubl. data) and gathered from the literature to give a more complete sample. These data and those of Parra (1978) are plotted in figure 1. For the purposes of this figure, we are considering only those foregut fermenters that do not ruminate (i.e., chew their cud). The regression is highly significant with a slope of 1.043. Demment (1982) discussed the bias of gut contents as an estimate of gut capacity and concluded that the actual relationship between gut capacity and body weight is likely to be isometric. Ruminants and nonruminants fit the same regression line.

If the metabolic rate determines the energetic requirement and the gut size determines the capacity to process food into nutrients, then the nonlinear response of metabolism and the approximately linear response of gut size produce higher ratios of metabolism to processing capacity in small animals than in large ones. Demment (1983) presented a simple kinetic model of this relationship and showed that, mathematically, retention time, T_r, for a food particle is related to body weight:

$$T_r = .589\, D\, W^{.28} \tag{2}$$

where D is digestibility of the diet and W is body weight (kg). While the first-order models have been widely used to model herbivore digestion (Van Soest 1982), all particles do not behave according to first-order kinetics. (Some aspects of this complexity are discussed in detail below.)

This formulation states that retention times, at the same factor of metabolism, will be shorter for smaller than larger animals when fed the same diet. Two assumptions are made in the model that do not hold in reality. First, food (plant material) is considered as homogeneous relative to digestion; and second, digestibility is constant relative to retention time. In the following sections, the effects of these assumptions will be discussed.

PLANT MATERIAL

Plant material is not homogeneous in its response to animal digestive systems. Chemical components of plants differ in their rates of digestion by vertebrate and microbial enzymes. Therefore, ideally, plant material should be characterized by the component fractions that show uniform reaction to digestive enzymes. To establish relative digestibility would then require the determination of the proportions of the component fractions in the foods. Chemical analyses, however, do not necessarily act on forages to separate nutritionally uniform elements (Van Soest 1982).

The major functional division of plant material is between the cell constituents and the cell wall. The contents of the cell are the fraction active in plant metabolism and are composed primarily of sugars, proteins, and storage carbohydrates. This fraction can be digested directly by vertebrate enzymes or fermented rapidly by microbes. The cell-wall fraction provides the structural matter for the plant that cannot be degraded by vertebrate digestion but can be hydrolyzed slowly by bacterial and fungal enzymes (Gibson 1968). Therefore, the use of the cell wall for a nutrient source is dependent on microbial symbiosis (Hungate 1966). The cell wall, while providing the plant with structural support, also functions to defend the plant against herbivores. Because the rapidly and slowly digestible components of forages are complementary fractions of the total dry matter, overall fermentation rate will generally decrease with increasing concentration of cell wall.

The availability of cellulose and hemicellulose for fermentation varies with the

TABLE 1

CHEMICAL COMPOSITION OF PLANT MATERIAL CLASSIFIED BY FUNCTION OF PLANT PARTS

FUNCTIONAL GROUPS	CHEMICAL (percent dry matter)*				*N*	SOURCE
	CW	HC	CEL	LIG		
Structural tissue						
Wood (trees)	88.1	22.5	45.4	20.2	6	Browning 1975
Bark (trees)	76.1	10.9	44.0	20.2	3	Van Soest & Robertson 1976
Stems						
Spring (trees & shrubs)	35.8	7.7	18.9	9.2	20	Short et al. 1975
Winter	61.9	13.1	29.1	19.8	20	Short et al. 1975
Tropical grass	74.3	29.6	35.3	10.1	9	Van Soest 1973
Temperate grass	60.7	28.4	29.5	2.8	2	Laredo & Minson 1975
Legume	54.0	9.8	34.6	10.4	22	Luckett et al. 1967
Photosynthetic surfaces						
Leaves						
Trees & shrubs	57.1	16.5	23.5	14.6	18	Robbins & Moen 1975
Tropical grass	66.3	32.7	27.4	5.8	9	Van Soest 1973
Temperate grass	55.4	29.0	23.6	2.8	2	Laredo & Minson 1975
Leaves & stems						
Temperate annual grass	59.0	23.0	29.8	6.2	15	Van Soest 1975
Storage organs						
Underground storage (domestic)	10.0	3.5	5.1	.8	5	Van Soest & Robertson 1976
Reproductive organs						
Seed hulls	76.0	15.3	47.9	13.5	6	Van Soest & Robertson 1976
Seeds with hulls	52.5	13.7	19.5	19.4	20	Short & Epps 1977
Seeds without hulls	17.8	7.1	5.4	9.9	5	Short & Epps 1977
Seeds (legume)	40.4	20.0	16.3	4.2	9	Short & Epps 1977
Fruits (fleshy, incl. seeds)	40.9	10.9	15.2	14.8	47	Short & Epps 1977
Fruits (domestic, no covering)	14.4	3.6	8.8	2.0	4	Van Soest & Robertson 1976

* CW = cell wall; HC = hemicellulose; CEL = cellulose; LIG = lignin.

lignin content of the cell wall (Van Soest 1967). The chemical basis for lignin's effects is unclear, but may involve the cross linkages that occur between the lignin and structural carbohydrates of the cell wall (Van Soest 1977). How much cell wall can be degraded is a function of the rate constant of digestion of the cell wall (i.e., the digestion rate), the retention time (how long the digestion rate operates on this cell wall), and the amount of potentially digestible cell wall in the forage (a function of its lignin content [Mertens 1973]). The effect of lignin on digestibility is only important when digestion rates and retention times would otherwise be sufficient to allow greater digestion of the cell wall.

Table 1 is a compilation of chemical analyses of plant materials grouped on the basis of their functions. Several interesting patterns are apparent. In general, there is a positive association between the permanency of a structure and its cell wall and lignin contents. Since plants usually put the most energy into the defense of more permanent parts (McKey 1974), and these structures are most likely to be supportive, both functions are likely to produce a positive relationship between permanence of the plant part and its cell-wall and lignin content. Therefore, herbivores are apt to be sensitive to differences between the functional categories of plant material when making feeding decisions.

Reproductive and storage organs have little fiber content when separated from their protective hulls that are high in cell wall and lignin. The fiber and lignin values for seeds (as well as their potential toxicity) often depress the overall nutritive value of fruits. The selective removal of hulls and seeds from fruits can increase the energy density of the reproductive plant parts. Storage organs or storage sites, however, are often located where they are difficult to harvest (i.e., underground) or within indigestible structures (i.e., stems in tropical grasses).

Tropical grasses have higher cell-wall and lignin concentration (and lower digestibility) than temperate grasses (Minson and McLeod 1970). Cell-wall formation and lignification are primarily affected by temperature, and this temperature response creates greater differentiation in forage quality between the stem and leaf fraction in tropical grasses (Deinum and Dirven 1975). The preponderance of C_4 grasses in the tropics accentuates the low-quality component in these ecosystems (Caswell et al. 1973).

Resource Axis: Fiber Curve

The availability of nutrients to the herbivore is a function not only of the chemical composition of the forage, but also of the spatial distribution and abundance of the nutrients. An understanding of availability requires that one consider the biomass of plant material in a habitat on the basis of its quality. Quality is defined in this model as the digestion rate of the forage (proportional to its cell-wall content) and the extent of its potential digestibility (proportional to its lignification). Therefore, initially, forage quality is considered as inversely related to the amount of cell wall and lignification.

Demment (1983) presented a model (a fiber curve) to describe the relationship between abundance and quality of foods for baboons and explored its implications for dietary changes with body size. A similar concept of a fiber spectrum as a

TABLE 2

FIBER CURVES: BIOMASS IN DIFFERENT HABITATS, BY PERCENTAGE IN CELL WALL

HABITAT	TONS/ HA	PERCENT OF BIOMASS IN CELL WALL								
		0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89
San Joaquin*										
Annual grassland										
11-25-74	.53		.04	.01		.48				
Bridger*										
Montane grassland										
6-12-72	1.71			.02	.10	.22	.08	.71	.56	
Bridger*										
Montane grassland										
8-22-72	3.19			.06	.52	.12	2.43	.02		
San Joaquin*										
4-25-74	4.59			.51	.12		3.96			
Hubbard Brook†										
Temperate deciduous forest										
Summer	161.50			2.81	.04	.50		.20	158.75	

* Data courtesy of US/IBP grasslands biome studies, Fort Collins, Colo.

† Biomass data from Whittaker et al. (1974). Chemical analysis: bark, Harkins and Rowe 1971; wood, Browning 1975; twigs, Short et al. 1972; leaves, Short et al. 1975; fruits, Short and Epps 1977; forbes, Short et al. 1974.

resource axis was presented independently by Foose (1978). Owen-Smith and Novellie (1982) used a comparable formulation based on protein content, cell contents, and cell wall to model ungulate diets. The fiber curve is a resource axis on which the cell-wall content is an index of digestion rate (the rate at which energy is released from ingested food). As the rapidly digesting cell contents are replaced by cell wall along the abscissa, digestion rate decreases. In this initial formulation, the effect of lignin is ignored. The density of biomass in frequency classes of percentage of cell-wall content (a fiber curve) for different habitats is presented in table 2. Table 2 was constructed by combining biomass and chemical composition data for functional categories with relatively homogeneous nutritional characteristics. For the grasslands, IBP data provided both the neutral detergent analysis (cell-wall content) and biomass data by plant species for specific sites and dates. The Hubbard Brook estimates were produced by obtaining cell-wall values from the literature for functional categories such as stemwood, bark, branches, twigs, leaves, etc., and assigning biomass values for these categories from Whittaker et al. (1974).

In this limited compilation some general trends are evident. With increasing standing crop, greater percentages of the biomass tend to be concentrated in the high-fiber categories. Within all habitats there is a general positive association of abundance and cell-wall content. This latter trend was observed in forest data by Lieth (1975). High-quality forage for herbivores is rare and low-quality is common. In the grasslands (one is annual and the other perennial in the temperate zone), the biomass shifts seasonally into higher-fiber categories. This response occurs because maturity and the late-season temperatures influence the cell-wall content of grasses (Deinum and Dervin 1971). A similar shift, but temporally more rapid, would be expected in tropical grasslands as accelerated early growth in conjunction with high temperatures increases cell-wall and lignin content after the seasonal rains. The distribution of biomass in fiber categories is spatially and temporarily dynamic, and herbivores can be expected to manipulate their food intake not only by dietary selection, but also by habitat choice and seasonal movement (e.g., Bell 1970; McNaughton 1978).

The values presented in table 2 indicate a general pattern, but are incomplete in certain aspects. The data necessary to construct habitat fiber curves are not widely available or detailed enough to consider important variability. For example, the grassland data for cell-wall content results from the analysis of the whole plant. Undoubtedly, there are differences in cell-wall content between plant parts on a scale distinguishable by mammalian herbivores. A small animal can eat a higher-quality diet than would seem possible by the estimates in table 2 simply by selecting parts at a finer grain than the nutritional analysis. Moreover, the peaks and valleys in such a curve may be accentuated because the natural variability between and within individual plant parts is removed.

Although the initial model used a linear relationship between abundance and quality (Demment 1983), for reasons discussed above, real fiber curves will probably show distinct changes in slope, especially in habitats where large quantities of relatively homogeneous nutritive value are present. In forests, where a great deal of the standing crop occurs as wood and leaves, a bimodal curve might

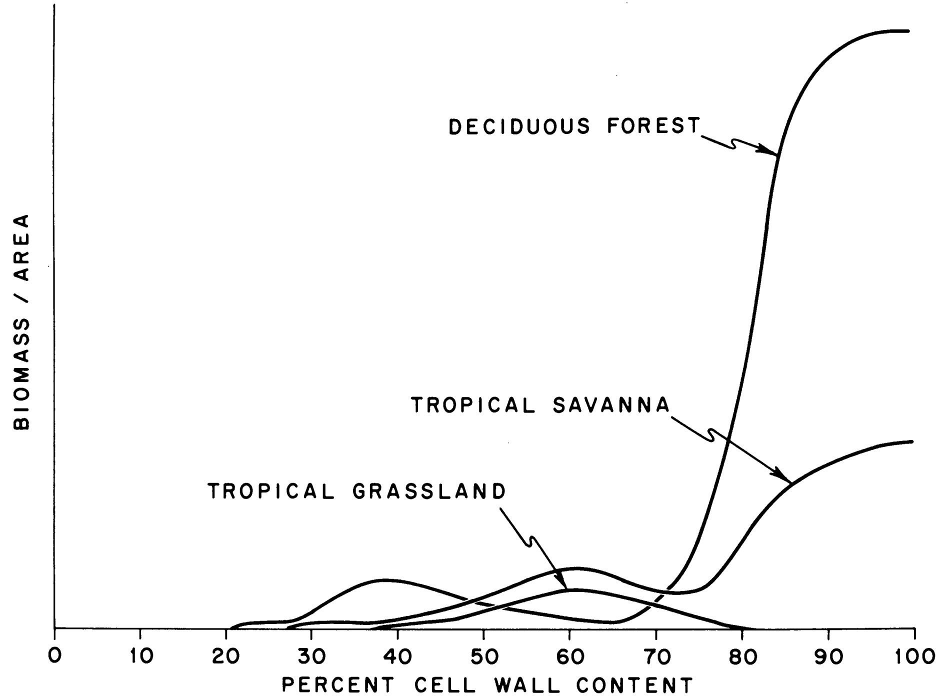

FIG. 2.—Fiber curves for different habitats are drawn as suggested by data in table 2.

be expected (fig. 2), as suggested by the Hubbard Brook data in table 2. In grasslands, where the majority of plant material has intermediate cell-wall content, the curve might rise and fall. As trees are added to grasslands, the curve would be expected to show elements of both the forest and grassland curves. The area under the curves represents the total biomass per area in the habitat.

Demment (1983) used the concept of a linear fiber curve to argue that baboon diets increased in fiber content more rapidly with increasing size. His analysis made the assumption that as body size increased, animals expanded their diets to include lower-quality foods. An increase in the fiber fraction means that proportionally more of the intake occurs in slowly digesting and indigestible fractions. At the same time, however, an increase in body size provides greater digestibility of the slowly digestible fraction. Therefore, the shape of the fiber curve in conjunction with the rate of change in digestive capacity with size will determine the functional relationship between body size and diet quality. An implicit assumption of the formulation is that with increasing body size, animals will expand their diets to include lower-quality foods. Alternatively, however, they could expand their feeding area and eat the same diet or feed longer. In reality, it seems probable that animals use all these alternatives. These trade-offs are important, and although the point needs further consideration, it is beyond the scope of this paper.

DIGESTIBILITY AND BODY SIZE

The digestibility of a forage is a function of the digestion rate acting on a particle for the duration of its retention within the gut. Using both in vitro and in vivo techniques, Smith et al. (1971, 1972) established that digestion rates were first order. Waldo et al. (1972) incorporated first-order kinetics in a digestion model in which rumen contents were divided into digestible and indigestible pool. Mertens (1973) tested the ability of a series of models to predict digestibility and intake and found Waldo's model with a discrete lag phase for the onset of digestion to be most satisfactory.

For our purposes, digestion rates are treated as rate constants. These rate constants are specific to the particular chemical fraction of the food, but are assumed to remain constant with body size. The assumption of constant digestion rate for cell contents assumes that the enzymatic activity of vertebrates is similar regardless of body size, and that vertebrate enzymes act at rates similar to those of microbes. The cell-wall fraction, because it is degradable only by microbial action, is assumed to be digested by microbes at similar rates, regardless of body size of the host or digestion site (foregut or hindgut). Higher fermentation rates recorded in smaller ruminants (Hungate 1966; Hoppe 1977) do not result from more-efficient microbial enzymes, but merely indicate that the food selected is composed of a greater proportion of rapidly fermentable components (Hoppe 1977).

Retention time is the most important factor in predicting intake and digestibility (Mertens 1973). Studies have demonstrated that digestibility can be depressed with high intakes (Raymond et al. 1959; Pearce and Moir 1964; Alwash and Thomas 1971, 1974; Tyrrell and Moe 1975). Tyrrell and Moe (1975) show that digestibility decreases linearly with increasing metabolic requirement in milking cows. Alwash and Thomas (1974) found retention times on all diets fed to sheep decreased with increasing intake, and the depression in digestibility was related to decreased retention times. Furthermore, particle size was positively correlated with retention time (discussed in more detail later) and digestibility.

Equation (2) predicts longer retention times with increased body size when the animals are fed at the same multiple of basal metabolism. Increasing body size should produce higher digestibilities because of longer retention times. The digestibility of roughage is higher in cows than in sheep on the same diet (Blaxter and Wainman 1964; Playne 1970; Prigge et al. 1984). The lower digestibility of roughages in sheep relative to cattle has been shown to be correlated with shorter retention times in the ruminoreticulum (Prigge et al. 1984). Van Soest et al. (1983) have summarized data on the relationship between body size, retention time, and digestibility of cellulose for a wide range of herbivores and show a positive correlation between these variables. Increased body size not only raises the digestibility of a forage, but also increases the total metabolic requirement of the animal. The fiber in the diet should increase with increasing body size at a rate dependent on the slope of the fiber curve.

In general, small animals that have high MR/GC ratios must eat food composed largely of a rapidly digestible fraction. Small nonruminants, however, can com-

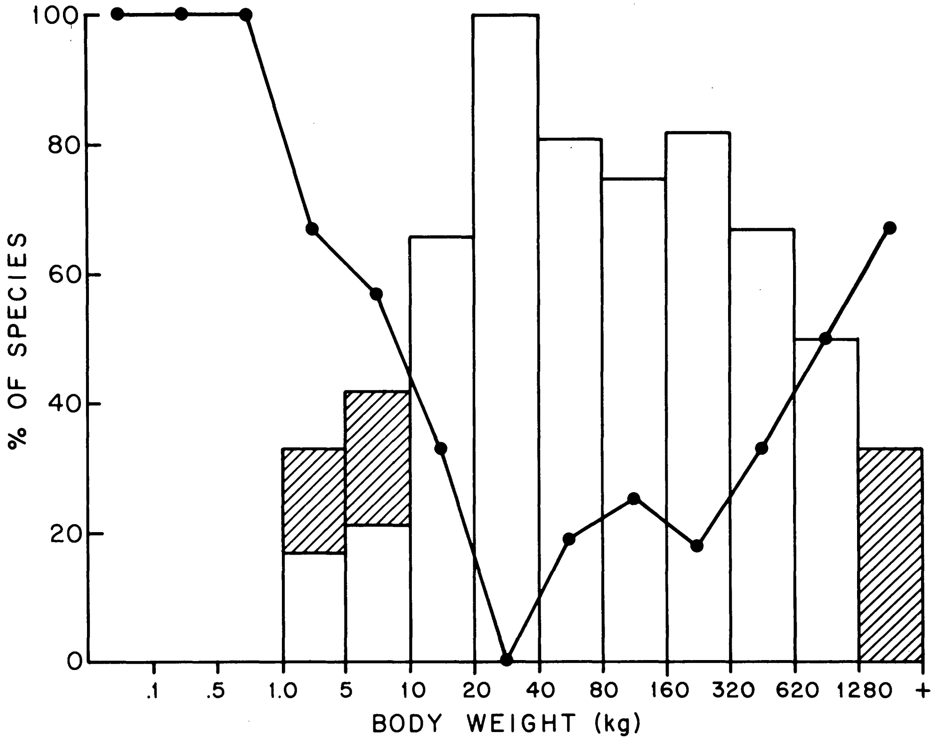

FIG. 3.—Percentages of 186 East African herbivore species that are ruminants (open histogram), nonruminants (solid circles), and foregut fermenters that do not ruminate (hatched histogram) are plotted in relationship to body weight. Data from Sachs 1967; Ledger 1968; Dorst and Dandelot 1969; Kingdon 1971; Clutton-Brock and Harvey 1977.

pensate for low quality to some degree by increasing intake (Batzli 1981). These small nonruminants show selectivity when faced with mature, fibrous plant material (Batzli et al. 1981). As the slowly digestible and(/or) indigestible portions predominate, increased intakes cannot compensate for the depression in digestibility (Baumgardt 1970). Keys and Van Soest (1970) found high mortality in voles (*Microtus pennsylvanicus*) fed pelleted diets of 55.6% and 62.7% cell wall when selectivity was not possible. Laboratory rats showed 30% mortality on diets of 38% cell wall and a rate of weight gain inversely correlated with cell wall in the diet (Keys et al. 1969). Small animals probably are limited by the time and energy requirements of finding rare high-quality foods required by their low digestive capacity or sufficient abundance of lower-quality foods to compensate with high intake. Since small animals have low total metabolic requirements, they have a greater ability to fulfill their metabolic requirements with rare high-quality foods than do larger herbivores. With increased body size, the total metabolic requirement increases and the animal expands its diet to lower-quality foods. Cows show a lower-quality diet than do sheep when grazing the same pasture (Dudzinski and Arnold 1973). In the dry season in the Serengeti, buffalo diets decrease in quality.

Because the buffalo must take in nutrients at some minimum rate, and it is impossible to maintain this rate by choosing rare high-quality leaves, they expand their diets to include lower-quality grass components (Sinclair 1977). They also catabolize body stores in the dry season. The extent to which the diet can be expanded is limited by the ability to process low-quality food (see section on large herbivores). The positive relationship between body size and home range (McNab 1963) indicates that animals also respond by using a larger area.

The evolutionary response of herbivores to these constraints has produced several digestion systems. The primary functional dichotomies are based on the location of the fermentation site (Foose 1978) and the existence of the rumination process. While all ruminants carry on fermentation in the foregut, nonruminants have fermentation sites in either the foregut or hindgut. The rumination process, as discussed below, is ecologically significant and should be distinguished from foregut fermentation alone.

Data on the relationship between digestive strategy and body size in East African nonforest herbivores indicate that ruminant species dominate the medium body sizes, while nonruminants are the prevalent small and very large herbivores (fig. 3). In the following discussion we consider how the constraints of body size may be responsible for this pattern and how differences in the physiology of digestion between ruminants and nonruminants result in differences in their feeding ecology. For ease of discussion, and keeping in mind that the range of body sizes is a continuum, we consider groups as small, medium, or large herbivores.

RUMINANT DOMINANCE OF THE MEDIUM BODY-SIZE RANGE

As body size increases, the reduction in the MR/GC ratio allows slower rates of passage of ingesta for the medium-sized herbivore. The longer retention times result in greater digestibility of the slowly digestible fraction of forages. The larger body size increases the total amount of energy required for maintenance (and locomotion per unit distance) and therefore, as Demment (1983) argued, increases the fiber content of the diet. The relaxation of the constraints of rapid passage, coupled with the greater metabolic requirements, is a prerequisite for the evolution of gut structures that selectively delay the passage of fibrous foods.

Foose (personal communication in Janis 1976) postulates that differences in digestive systems resulted in the radiation of the artiodactyls at the expense of the perissodactyls when the grasslands expanded in the Tertiary. In the present tropical grasslands and savannas, the medium-sized ruminants dominate by feeding on forage that contains most of its energy in the fermentable fraction of the cell wall. A comparison of feeding trials (fig. 4) on similar-sized herbivores (cows and horses) indicates similar digestion capabilities for low-fiber foods, but increasing relative efficiency per unit of intake for the ruminant on higher-fiber diets. The differences in efficiency reflect the effect of selective delay in the rumen.

The rumen functions more efficiently (nutrients extracted per unit intake) than does the cecum or colon because of its selective delay of forage. Selective delay reduces the probability that food recently ingested will pass out of the rumen incompletely digested. Consider a volume within which perfect mixing occurs.

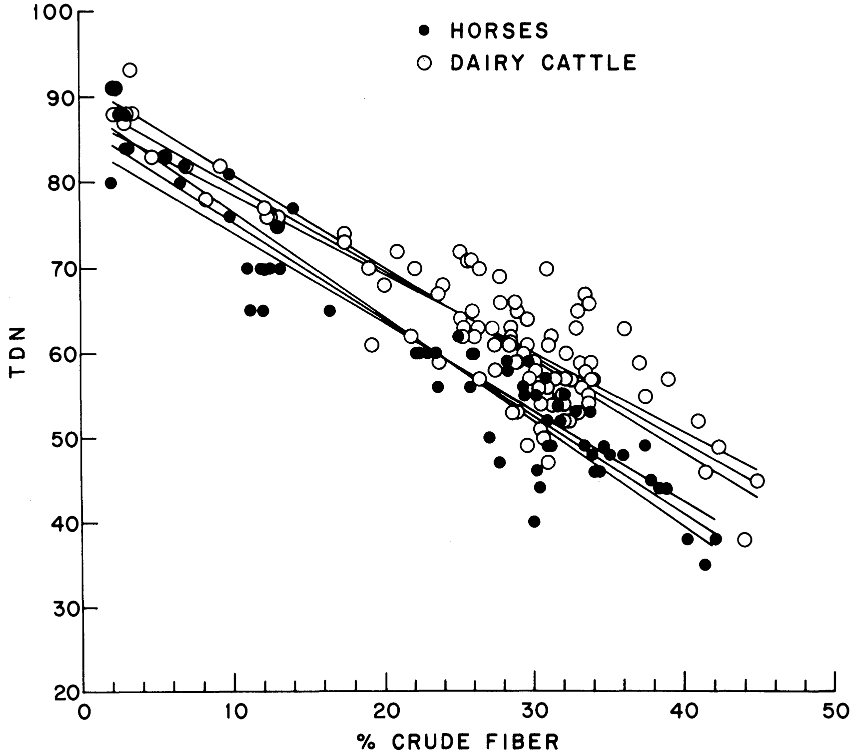

FIG. 4.—Total digestible nutrients (TDN) of foods for horses and dairy cattle are plotted against their crude-fiber values. Data are from digestibility trials and crude-fiber assays reported by the NRC (1973, 1978). Foods which received processing (i.e., grinding) were excluded. The slopes of the regression equations are different ($F = 7.019$; $V_1 = 1$, $V_2 = 170$; $P = .018$). 5% CI on the slopes of the regression lines are shown.

Once a particle enters the volume, the probability that it will be passed is constant with residence time. The rumen has a mechanism to ensure that the probability of passage increases with residence time. In figure 5 we use data from Smith (1968) to show calculated passage rates as a function of particle size in sheep. Large particles have very low passage rates. As particles are reduced in size, their probability of passage increases. (Very small particles of less than 200 μm and of high specific gravity sink to the bottom of the rumen and are retained for long periods [J. Welch, personal communication].) Therefore, the efficiency of the rumen is produced by linking probability of passage to residence time in the rumen (and thereby, extent of digestion) via particle size. Since the cecum and colon, although somewhat selective in retention (Stevens et al. 1980), cause particles to behave more like perfect mixing, more particles are lost before complete digestion. The actual mechanism for the selective delay in the rumen has not been identified.

The greater efficiency of energy extraction of the ruminant digestive system for

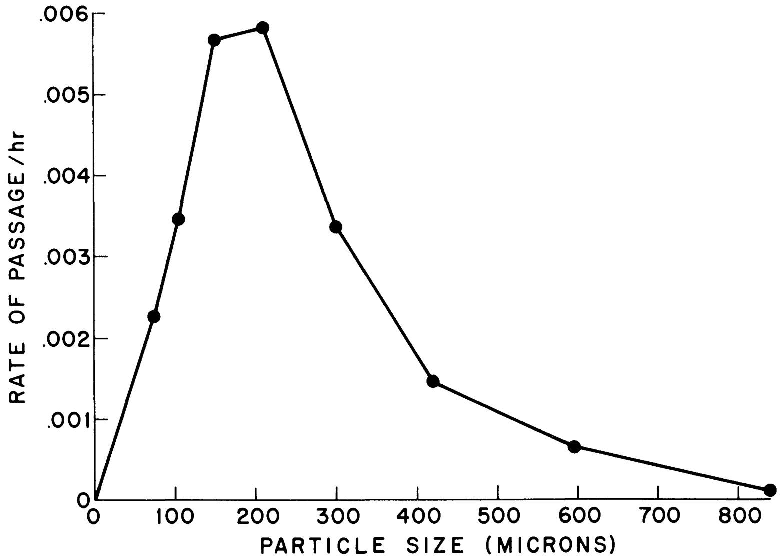

FIG. 5.—The passage rate of particles from the rumen of sheep is plotted as a function of their size; data from Smith (1968).

conditions encountered by the medium-sized grassland herbivore appears to be limited to a range of body sizes (fig. 3). Of importance to the discussion of the role of body size and its possible effect on competition are the factors that limit the range of body sizes over which one particular morphological strategy is more efficient than another. In this context, those factors that constrain the ruminants in the small and large body sizes are considered.

CONSTRAINTS ON SMALL RUMINANTS AND THE EFFICIENCIES OF SMALL NONRUMINANTS

The constraints imposed by a high *MR/GC* ratio should affect the ability of smaller ruminants to delay the passage of ingesta. The absence of morphological adaptations for delay in the small African antelope are discussed extensively by Hofmann (1973). Besides the finer morphological adaptations to rapid passage, the rumens of small antelope studied by Hofmann show gross structural design necessary for rapid transit.

Small ruminants must compensate for the proportionately greater *MR/GC* ratio by higher rates of energy production per unit volume of the rumen. Hoppe (1977) measured the fermentation rates of wild East African antelope in the dry season. His data are converted to energy production per day for the rumen of each species (table 3) and plotted with different isoclines of metabolism in figure 6. The calculations show that energy available above basal metabolisms increases with size within this group. If the foregut produces 97.8% of all volatile fatty acids (VFA) in the gut (Hungate et al. 1959), then African antelope below 9.4 kg do not balance basal energetic requirements in the dry season on VFA production.

TABLE 3

ENERGY PRODUCED BY FERMENTATION IN THE RUMINORETICULUM OF EAST AFRICAN ANTELOPE

Species	Body Wt (kg)*	Rumino-reticulum Content (kg *DM*)†	Energy Content of VFA (kcal/mole)	Fermentation Rate (moles/kg *DM*/day)*	Fermentative Energy Production of Ruminoreticulum (kcal/day)‡
Nesotragus moschatus	3.6	.05	279.4	13.74	191.9
Rhynchotragus kirki	4.2	.04	281.6	13.28	149.6
Raphicerus campestris	10.5	.12	274.8	10.85	357.8
Sylvicapra grimmia	13.0	.20	257.9	10.36	534.7
Gazella thomsoni	18.0	.32	250.6	9.64	773.0
Tragelaphus scriptus	27.0	.28	260.0	8.82	642.1
Gazella granti	49.0	.66	255.8	7.73	1305.0
Aepyceros melampus	51.0	.59	262.1	7.66	1184.5
Damaliscus korrigum	114.0	1.94	283.1	6.42	3526.0
Alcephalus buselaphus	120.0	2.08	267.8	6.35	3537.1
Connochaetes taurinus	200.0	4.23	270.5	5.68	6499.1

* Body-weight data, Hoppe 1977; fermentation rate for regression equation on wild species (i.e., those included in this table), Hoppe 1977.

† Dry weights from Hoppe (personal communication).

‡ Energy value of a mole of VFA calculated on the basis of VFA composition of ruminoreticulum sample (see Leng and Brett 1966). Caloric values used for acids are acetic, 209 kcal; propionic, 367; iso- and n-butyric, 524; iso- and N-valeric, 628.

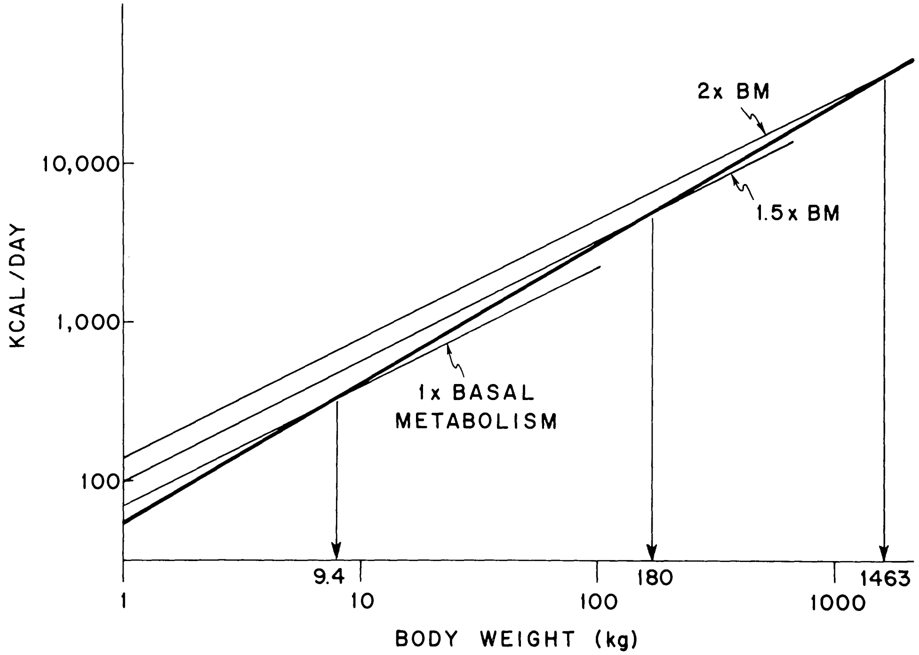

FIG. 6.—Rate of fermentative energy production of the rumen calculated in table 3 is plotted against weight. Isoclines of multiples of basal metabolic requirement relative to body weight are drawn to show weights below which these levels of metabolism cannot be supported on energy production of the rumen.

Fermentation rates are a function of food quality and intake rates. Food quality affects the proportion of substrates that are digested slowly in the rumen. Moreover, high-quality foods probably provide a balanced nutritional environment within which microbial digestion can more closely approach its maximal rate. Hoppe (1977) interprets the negative correlation between fermentation rate and body weight as a decrease in the proportion of dicotyledons to monocotyledons in the diet as body size increases.

Intake can affect fermentation rates because, like diet quality, it can determine the proportion of different substrates in the rumen. The rapidly fermentable fraction is underrepresented in the rumen relative to the total diet because it is being digested quickly. As intake is increased, the proportion of the fractions in the rumen approach those in the diet. At that point, no greater energy production rate can be achieved on that mix of forages. Initial modeling of this problem (M. Demment and T. Starr, in prep.) indicates that the response of energy production to increasing intake is curvilinear, asymptotic at the point at which diet and rumen fractions are equal. These results suggest that increasing intake yields diminishing increases in energy production. Two factors constrain the ability of small ruminants to respond by increasing intake. First, since high-quality foods are rare, their ability to maintain high levels of intake is limited by their ability to find these foods. Second, the small ruminant is limited in its ability to expand its diet to more common, lower-quality foods. Any potential increases in energy production resulting from greater intake would be affected by decreases in energy production caused by diminished dietary quality.

Hoppe's data (1977) give an integrated measure of all factors determining the fermentation rate and are therefore likely to reflect a realistic energetic picture of this group during the dry season. Fermentation rates, however, may not be the entire energy source for small ruminants. Orskov et al. (1969, 1970) have shown that diets that pass rapidly through the rumen provide soluble energy sources to the lower tract. Therefore, small herbivores may derive progressively larger amounts of energy from direct digestion in the abomasum. As an herbivore moves to a strategy of allowing greater escape to the lower tract, however, the digestive system acts less like that of a ruminant.

Kinnear et al. (1979) suggest that in the very small (=2 kg) macropods that possess foregut fermentation, there may exist selective direction of ingesta to areas of the stomach for either fermentation or gastric digestion. If this physiological adaptation is not available to small animals, then with decreasing size the required diet will be used more efficiently by direct digestion. Black (1971) modeled a comparison of ruminant and nonruminant lambs (=20 kg). On diets of low fiber and high protein, he calculated that the nonruminant model had 39% to 45% more energy available for maintenance and 22% to 61% more for production (i.e., growth, wool). His model indicated that a dietary level of 22% crude fiber was necessary before the ruminant lamb was more efficient. These calculations emphasize the obvious point: if the diet contains a large portion of soluble nutrients, fermentation extracts less energy than direct digestion. Fermentation in the foregut for food of low fiber content unnecessarily places another trophic level between the herbivore and its food supply. The costs of heat and methane production can reduce energy assimilated by the herbivore by 20% of what is digested. Only when an appreciable amount of energy is present in the cell-wall fraction does fermentation in the foregut become advantageous. Hoppe's data demonstrate that animals below 9.4 kg must receive substantial energy from sources other than fermentation (i.e., direct digestion, body stores) in the dry season. These calculations suggest that fermentation rates may be an important constraint on the lower limits of ruminant body size in the African savanna.

The solution for the small animal is to digest the soluble fraction directly in the foregut and ferment the cell wall posteriorly. The gut microbes do more than make the energy of structural carbohydrates available to the herbivore. Microorganisms provide the small animal with essential nutrients (McBee 1971), such as the B-vitamins and amino acids which are synthesized from ammonia nitrogen. Luckey et al. (1955) demonstrated that germ-free rats (i.e., rats whose intestinal microorganisms had been removed with antibiotics) required vitamins that conventional rats received from microbes. Evidence of B-vitamin synthesis has been reported in rats (Barnes and Fiala 1958), rabbits (Huang et al. 1954), pigs (Howie and Baker 1952), and horses (Carroll et al. 1949).

For the herbivore, the major energy sources from fermentation are the waste products of microbial respiration, VFA, which are absorbed directly by the host. Most of the dietary nutrients which enter the fermentation site are assimilated by the microbes and used either for respiration or for synthesis of organic compounds which are incorporated into microbial tissue. The recovery of these nutrients requires the digestion of microbial bodies and the absorption of the resulting nutrient components. The digestive process cannot occur within the fermentation site because the change in pH required for digestion would depopulate the organ. For this reason, a digestion and absorption site must be present posterior to the fermentation site to reclaim these nutrients. Furthermore, sufficient time must be available to allow for digestion and absorption before defecation occurs. Therefore, the positioning of the fermentation site (anterior vs. posterior) and the size of the animal (which determines its retention time) are important factors constraining herbivores' ability to recover microbial nutrients.

The small animal has, in an evolutionary sense, traded off the high fecal nutrient losses (primarily of microbial origin) for the greater efficiency of direct digestion of this diet by the nonruminant system. To counteract this disadvantage, small animals practice coprophagy, which allows the reingestion of fecal material for direct digestion and absorption of nutrients in the foregut. Coprophagy is common in the rodents and lagomorphs (McBee 1977), has been reported in primates (Hladik et al. 1971; A. Vedder, personal communication), and occurs in horses under dietary restrictions (Willard et al. 1973). The efficiency of coprophagy is increased by production of either soft or hard feces. The soft feces in the rabbit are low in fiber (Uden 1978) and high in protein and B-vitamins. The protein content of soft feces was 28.5% in the rabbit (Kulwich et al. 1953); similar values for soft feces are reported by Huang et al. (1954) and Griffiths and Davies (1963), while the hard feces contained 9.2% protein. The concentration of vitamin B-12 in the feces of rabbits was 221 times that in the diet (Kulwich et al. 1953). Tadayyon and Lutwak (1969), working with rats, observed that coprophagy improved the use of poorly absorbed fats and increased the intake of calcium, magnesium, and phosphorus.

The role of the microbial synthesis of nutrients may be of major importance in the evolution of hindgut fermentation in small herbivores. The high *MR/GC* ratio of this group argues strongly that hindgut fermentation has not evolved primarily to supply energy. The volume of the gut devoted to fermentation of the slowly digesting fraction could supply energy more efficiently if it were redistributed to the foregut and used for direct digestion of rapidly digesting soluble nutrients. The synthetic capability may be of importance in extending the range of foods and environments used by small mammals (Kinnear et al. 1979).

CONSTRAINTS ON LARGE RUMINANTS AND ADVANTAGES OF VERY LARGE NONRUMINANTS

In this section, we suggest that the upper limits on ruminant body size are influenced by the ability of herbivores to maintain adequate intake on low-quality forages. Because intake is the most important factor affecting productivity in domestic herbivores (Reid 1961), one of the central themes of ruminant research has been to determine factors that influence intake under different dietary regimes.

Early research on several herbivorous species showed their ability to increase the intake of concentrate diets, progressively diluted with a nutritionally inert substance, until the diets reached a dilution level at which lower intakes were observed (rats, Peterson and Baumgardt 1971; chickens, Mraz et al. 1957; sheep, Weston 1966; cattle, Conrad et al. 1964). The initial response to decreasing caloric density has been labeled a physiological response to balance energy requirements, while the depression in intake is interpreted as a response to the volumetric limits of the gut or rumen (Baumgardt 1970; Baile and Forbes 1974).

The observation that the amount of digesta in the gastrointestinal tract and the rumen is a relatively constant maximal value, regardless of dilution source, has led to the concept of fill models (Blaxter et al. 1961; Campling et al. 1961). These models predict intake on the basis of the determinants of rumen fill. From the simple concept that the volume of the rumen limits intake (Adolph 1947), the models have developed into formulations of processes that determine rumen fill (Ellis 1978). The importance of a particular parameter in determining intake varies with the conditions of the experiment, and since the upper limits on the size of ruminants are the focus (i.e., animals that eat low-quality diets), the following discussion concentrates on the limiting factors on roughage diets.

Recent work with natural forages, which vary widely in digestibility, has produced results contrary to work with dilution diets. Both Mertens (1973) and Osbourn et al. (1974) found that the intake of sheep was linearly related and highly correlated ($r = -.76, -.83$, respectively) with cell-wall concentration. In contrast to the work described above, there was no indication that animals restricted their intake on high-quality foods just to balance energy requirements. In fact, using data from 179 forages, Mertens (1973) found that animals eat to a constant cell-wall intake (g CW/day). He interpreted the importance of the cell-wall correlation, as had Van Soest (1967), as an indicator of the volumetric characteristics of the forage. In recent unpublished work, P. Van Der Aar (in Van Soest's laboratory) has measured the volumetric properties of the forages used by Mertens (1973). Van Der Aar found a low correlation ($r = -.43$) between bulk volume and intake. His examination indicates that the volume of forages is determined by the cell-wall structure in early growth stages. As the plant matures, the cell volume does not change but the cell wall thickens. Therefore, the density and percentage dry matter of the cell wall increase with age. These results raise questions about the interpretations of Van Soest (1967) and Mertens (1973) that there is a strong volumetric relationship between cell-wall content and bulk volume of forages which, in turn, produces the high correlation between intake and cell-wall content.

If cell-wall content is not a good measure of bulk volume, then why is cell-wall content a good predictor of intake? If the rumen works as a filtering system, which Smith's data (1968) suggest, then intake should be related, especially on low-quality forages, to the ability to move ingesta through this filter (i.e., relieve fill). Mertens (1973) evaluated the ability of fill models to predict the intake values he measured. He concluded that passage rate is a more important determinant of fill than digestion rate. Rate of passage can be increased either by increasing the rate of particle breakdown or by increasing the size of particles which escape the rumen. Although little is known of factors affecting the latter, particle breakdown occurs by the processes of rumination and digestion. Troelsen and Bigsby (1964) found a high correlation between the particle sizes produced by artificial mastication of a forage and its intake. More recently, cell-wall intake has been shown to be highly correlated with rumination time of sheep and cattle on a wide range of forages (Welch and Smith 1969, 1970). These results suggest that the link between intake and cell wall exists because the rate at which particles can be broken down is constant relative to their cell-wall content.

These interpretations indicate that the same mechanism (selective delay based on particle size) that provides the greater efficiency per unit of intake for ruminants on diets of intermediate fiber content is also the one that may limit their ability to function well on high-fiber diets at high levels of intake. Welch (1979, personal communication) has examined rumination capacity in two contexts. First, he measured rumination rates of sheep, goats, and cattle fed a single meal of hay preceded by 2 days of fasting. Rumination rate is calculated by dividing the measured intake of cell wall (g) by the rumination time. These data show that rumination rate (y, g CW/min) is related to body weight (x, kg) by the following regression equation:

$$\log y = .96 \log x - 1.69 \qquad r = .92.$$

In a second series of trials, cattle were fed ad libitum. Rumination rate was related to body weight as

$$\log y = .63 \log x - .68 \qquad r = .73. \tag{3}$$

Both equations indicate a decreasing ability to ruminate cell wall with increasing body size; however, the exponents are considerably different. Since the primary concern is to relate body size to the ability to relieve rumen fill, the fasting trials are probably not appropriate because during the fasting the animals are likely to be emptying their rumens. In this case, intake will reflect more the empty volume of the rumen than passage, and the rumination rate will not reflect particle breakdown necessary for passage. The trials may also differ because of the difference between inter- and intraspecific relationships. In the ad libitum trials, rumination rates on the high-fiber diets are likely to reflect the animals' ability to relieve rumen fill. The ad libitum data may be limited, however, because the animals are not being pushed to ruminate at their maximum capacity. Nevertheless, with these considerations in mind, the ad libitum data have been selected as the most appropriate for the following examination.

Qualitative evidence has indicated that some ruminants, particularly the grazers, are adversely affected by low-quality diets. Hofmann (1973) reports the impaction of the rumen on coarse diets. Within a species, as dietary quality decreases, the ratio of rumination to feeding time increases. African buffalo in the Serengeti have a ratio of rumination to feeding time of .75 in the wet season, but in the dry season the ratio increases to .94 (Sinclair 1977).

Adequate data are not available to examine interspecifically the relative rates of change in rumination capacity relative to dietary cell wall with increasing body size. Sufficient data, however, are available to consider the effect of body-size increases on the African buffalo. Since the buffalo is the largest grazing ruminant in the African grasslands and savannas, factors limiting its size may constrain the upper size of ruminants in general.

Buffalo prefer a diet of grass leaves followed by sheaths and stems (Sinclair 1977). In the wet season when leaves are abundant, they form the majority of the diet and decline in importance as the dry season advances (Sinclair 1977). Sinclair proposed that as the density of leaves decreases, buffalo cannot maintain their required rate of intake on these rare items and expand their diets to eat the more abundant (but less digestible) stems.

Using this same logic, the cell wall (g) in the diet of a hypothetical buffalo (of greater than actual size) was calculated by assuming that the energy required for increased size would come from the selection of grass stems (see Appendix). Since October is the height of the dry season, the calculations used values for this month as the worst-case situation for the buffalo. In this month, the dry-matter cell-wall content of the diet, CW_t (g *CW*/day) is $CW_t = 61.7\, w^{.75} - 539.5$. (This result is the same as equation [A6] in the Appendix.)

J. Welch (personal communication) has found that domestic cattle and sheep cannot be forced to ruminate longer than 10 h per day. Using this value as the maximum rumination time possible for buffalo, the amount of cell wall (g) that can be processed in this period can be calculated from equation (3). The total cell-wall content of the diet of buffalo of increasing size can be estimated by equation (A6). At approximately 655 kg, buffalo cannot ruminate sufficient cell wall to balance metabolic requirements. This weight, 655 kg, is smaller than the largest of the buffalo sampled by Sinclair (1977; 690 kg).

Although our objective is to suggest that rumination rate and declining dietary quality are a limit on the upper size of ruminants, the calculations presented above should be viewed cautiously. First, the two regressions used have sufficiently similar slopes so that small changes in the constants of either equations will produce substantially different solutions. Second, because the body composition of animals changes with size and age (i.e., proportion of muscle and fat), intraspecific exponents relating weight to metabolism vary from .75 (Thonney et al. 1976). Therefore, although the .75 exponent seems appropriate for the calculation in an evolutionary framework, it may not be acceptable when applied to the buffalo in a practical context. Third, as well demonstrated by Sinclair (1977), the body stores are used by large animals as a strategy to deal with reproduction in a fluctuating environment. Therefore, comparison of weight prediction with field data are approximations with a great deal of variability, an inherent biological property of the animal.

If retention times increase with body size, and digestibility is a function of retention time, then as body size is increased, a point is reached at which complete digestion of the potentially digestible cell wall will occur even without selective delay of ingesta (i.e., perfect mixing). This factor may be an additional reason for the lack of many large ruminant species. To examine this hypothesis requires a function expressing the rate at which forages digest when in contact with microbes.

Because large herbivores have retention times much longer than those required for complete digestion of the soluble fraction, and because their diets are composed primarily of cell wall, this discussion focuses on the digestion rates of the fiber fraction. Since cell walls are digested by microbial fermentation, T_r (retention time) must be calculated for the fermentation site and not the entire gut. The net weight (kg) of the fermentation site contents, F, can be calculated from a regression against body weight, W (kg) (Parra 1978), but keep in mind that ruminants and nonruminants fit the same regression line: $F = .0761\ W^{1.096}$. The T_r (h) of the fermentation site can be calculated for an animal at 1.5 times basal metabolism by dividing, as above, F by the intake required by metabolism:

$$T_r = 7.67\ D\ W^{.346} \tag{4}$$

where D is the digestibility of the intake. The dry weight of the contents was estimated as 10%.

We now link the energy production of ingesta, its volume, and retention time within the fermentation site. The volume of a forage is primarily composed of its structural components. Smith et al. (1972) have shown that the cell wall can be separated into digestible and indigestible fractions and that digestion (in vitro) of the digestible fraction occurs as a constant proportion per unit time. The indigestible portion can be estimated by the fraction remaining after no change in forage mass is observed; in this case 72 h after initiation of the digestion trial.

If digestion of the digestible cell wall, CW_D, proceeds according to first-order kinetics, then the amount of CW_D remaining at some retention time, t_r, after digestion begins is

$$CW_D\ (t_r) = CW_D e^{-rt_r}$$

where r is the rate constant of digestion. If the digestion of a unit mass of forage produces a quantity a (4409 kcal/kg), then the digestible energy, DE, produced at t_r is the derivative of $CW_D\ (t_r)$ converted to kcal per unit time:

$$DE\ (t_r) = a\ CW_D(0) r\ e^{-rt_r}.$$

In this case, the loss of mass is positive energy for the herbivore. Therefore, DE (t) is a positive term because the constant, a, is a negative.

The volume of a unit of intake, V, decreases through time as

$$V\ (t_r) = V_0 - CW_D\ (1 - e^{-rt_r})$$

where V_0 is the initial intake volume. Therefore, the energy production of a unit volume of forage cell wall, E_{CW}, can be formulated as a function of the length of time it has been resident in the rumen, the retention time (t_r):

$$E_{CW}(t_r) = a \frac{CW_D\ r\ e^{-rt_r}}{V_0 - CW_D\ (1 - e^{-rt_r})}. \tag{5}$$

Using the in vitro fermentation data from Smith et al. (1972) for 32 forages, average values were calculated for r and CW_D for early and mature legumes and grasses (within-group values were consistent). Figure 7 shows the values of $E_{CW}(t_r)$ calculated for these forage classes. This figure indicates that the energy production of a unit of forage is always a decreasing function of retention time, and therefore the maintenance of high intake will always produce higher digest-

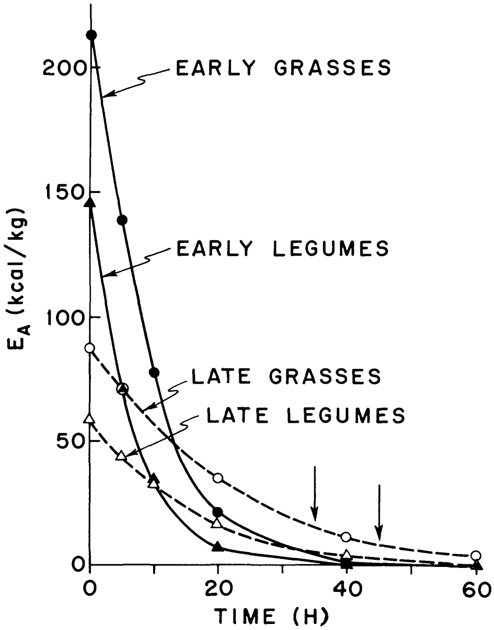

FIG. 7.—Energy production of the digesting cell walls of forages (kcal/kg) is plotted against retention time (h); data from Smith et al. (1972). Most of the energy in a unit of intake is released by 35 to 45 h (arrows).

ible-energy values for a unit of rumen volume. Intake is limited by the availability of forage and, for ruminants, potentially by the rate at which forage can be reduced to small particles. The question raised here is, At what point does body size become sufficiently large to produce retention times long enough so that a unit volume of ingesta is producing little energy? Approached qualitatively, an answer can be obtained by indicating the range of t_r in figure 7 where the energy present in a unit volume of intake has been almost completely removed. If complete digestion is considered to be 72 h, then the percentage of total energy available that has been digested at t_r can be calculated. Of the forages given by Smith et al. (1972), all reached 90% maximum digestion before 40 h. The arrows in figure 7 indicate a range of retention times, chosen qualitatively, when little energy remains to be digested by further retention within the fermentation site. Obviously, a consideration of optimal retention times must include aspects of forage availability, harvesting rates, and resource distribution.

In figure 8, the retention time has been plotted against body weight according to equation (4) for forages of different digestibilities. The retention times indicated by the crosshatching are those from figure 7 corresponding to the range of complete digestion values. These values indicate that at a dry-matter digestibility of 50%, forages with rapid digestion rates show complete digestion in animals of greater than 600 kg. Forages with very slow digestion rates require an animal of greater than 1200 kg for maximal digestion. The extent to which perfect mixing

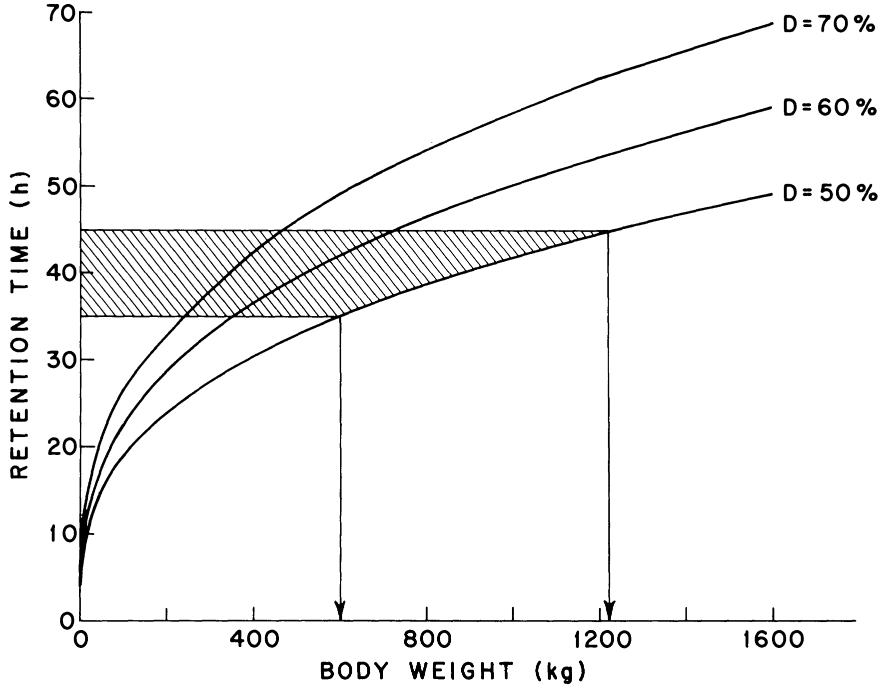

FIG. 8.—Retention time of foods in the fermentation chamber is plotted as a function of weight for foods of different digestibilities. Shaded area indicates retention time necessary to digest almost all the energy in a forage (see fig. 7) and the corresponding range of body sizes for this range of retention times when the digestibility of the food is 50%. If foods are 50% digestible and retention time is 45 h, then an animal of 1200 kg will show maximum extent of digestion of the food regardless of whether the fermentation site has selective delay or perfect mixing.

does not occur in the fermentation site will decrease the body sizes of these estimates. Nevertheless, given our assumptions and depending on the mix of forages, animals larger than 600 kg to 1200 kg will show equivalent digestive abilities, regardless of whether they are capable of highly developed selective retention or not.

The absolute magnitude of the metabolic requirement of large herbivores constrains them to a high-fiber diet, which is difficult to ruminate (a process necessary for selective retention). At the same time, their weight-specific metabolic requirement decreases to levels at which retention times make selective retention unnecessary. These findings suggest reasons for the upper limits of ruminant body size and the predominance of nonruminants among the largest herbivores.

DISCUSSION

The data presented indicate that along a continuum of body sizes, from small to large herbivores, digestive capacity and total metabolic requirements increase.

The fiber composition of plant material is the scaling variable for the resource axis, and abundance of food items with different fiber content can be plotted for individual habitats (a fiber curve). If competition is important in structuring communities (Diamond 1978), then body size is a factor providing a mechanism by which herbivores can differentially use this resource axis. Body size provides asymmetry in competition effects for digestive capacity of fiber (small animals always at a disadvantage), but may be balanced by the restriction resulting from the metabolic requirements of large animals. Herbivores are constrained to a range of foods on a particular fiber curve on which the lower limits (i.e., low fiber) are determined by abundance and the upper limits by digestive capacity. The relationship is similar in concept to that discussed by Wilson (1975) for predators, except that the resource-axis variable is different.

Although body size is considered an important variable for predicting feeding behavior and digestive strategy, its power, in this respect, can be diluted. Once there has been an initial evolutionary response involving body size (such as the evolution of the rumen), then body size becomes less capable of predicting feeding differences because the effects of size are confounded with those of gut anatomy. This point is reflected in figure 4. Cattle and horses, approximately equal in weight, have different digestive capacities. Body size is viewed as an important background evolutionary force that imposes constraints on what is possible for a given size. Within a range of responses, anatomical and behavioral differences can produce multiple solutions.

This point can be illustrated by the evolution of the horse. Janis (1976) attributes the evolutionary size increase of horses to both the evolution of ruminants and the increased fiber composition of forages as a response to climatic change. The constraints on small herbivores enumerated in this paper, considered in conjunction with morphological characteristics of the rumen of small antelope (Hofmann 1973), suggest that early ruminants possessed foregut fermentation for reasons other than fiber digestion. The spread of the grasslands created an environment where ruminants could more efficiently graze the available forages by increasing their size and further modifying their gut. Constraints on the ability of ruminants to process high-fiber foods may have limited the upper range of this body-size response. Unrestricted by their gut morphology, horses' tolerance to high fiber is set by body size. They probably responded to this competition by increasing their size to a point at which they could eat higher-fiber diets than could the ruminants because their intake was not restricted by the rate of particle-size breakdown. When the body-size effect is confounded by differences in digestive strategy, however, it alone is insufficiently precise an indicator to predict feeding differences (Milton 1981).

The model treats the *MR/GC* ratio as the primary determinant of body-size evolution and feeding behavior. A great number of biological parameters vary systematically with body weight (see Western 1979; Peters 1983) and the evolution of body size is an integrated response. Thus, the singular emphasis of this paper is a result of the focus of the paper, not a contention of exclusive importance. Similarly, feeding behavior is treated as a response to only digestive capacity and food abundance. In reality, an animal has nutrient-storage capabilities that allow excess nutrients from an abundance of food to be carried over to periods of scarcity or high metabolic demand. Interestingly, the storage capabilities of animals are an isometric function of body weight. If short-term capacity is considered to be gut fill, and long-term considered to be body stores (isometric with weight, Kleiber 1975), then the time an animal can maintain itself on each of the sources increases with body weight as a fractional power. In fluctuating environments, this body-size effect can be an important determinant of the species composition of permanently resident herbivores (Sinclair 1975).

SUMMARY

The gut capacity of mammalian herbivores increases linearly with body weight. This relationship, coupled with the change in basal metabolism with weight, produces an *MR*/*GC* ratio (metabolic requirement/gut capacity) that decreases with increasing body size. Since the retention of a food particle within the gut is proportional to this ratio, the extent to which food particles are digested will be related to body size.

Plant material is made up of chemical components that react differently to digestive enzymes. The fiber fraction of plant material (i.e., cell wall) is digested slowly and exclusively by microbial symbiotes. A positive relationship probably exists between the fiber content of plant parts and their biomass in the environment. This relationship is used to describe a resource axis on which digestion rate is the scaling variable. In response to this resource axis and metabolic requirements, the fiber content of the diet of herbivores increases with body size.

Ruminants are the predominant medium-sized herbivores in East Africa, while nonruminants are mainly small or very large animals. Small herbivores are constrained to rapid passage of ingesta by their high *MR*/*GC* ratio. In response, they have evolved hindgut fermentation and feed selectively on rapidly digestible (i.e., low-fiber) foods. Both responses contribute to loss of nutrients (synthesized by gut microbes) in the feces, and thus contribute to coprophagy in this group. To eat a diet higher in fiber, the herbivore must increase its body size. The reduced *MR*/*GC* ratio of medium-sized herbivores allows the evolution of gut structures that selectively delay the passage of ingesta. Selective delay results from the rumination process because the probability of passage is tied to particle size. This process produces more efficient fiber digestion in ruminants than that in nonruminants of similar size. Rumination, however, is advantageous over only a limited range of body sizes. The lower limits of ruminant body size are set by maximal fermentation rates. Foregut fermentation will not only digest the cell wall, but also use many of the soluble nutrients before their direct absorption is possible. Therefore, ruminants must rely almost entirely on the production of microbial volatile fatty acids (VFA) for energy and postruminal digestion of microbes for other nutrients. With decreasing body size, the increasing rate at which energy must be produced per unit volume of the rumen cannot be matched by a concomitant increase in the fermentation rate of forages. Nonruminants are favored by the more efficient energy transfer of enzymatic digestion in the foregut of the low-fiber foods often required by small animals.

The upper limits may be imposed by two factors. First, rumination rates (g cell wall ruminated per unit time) increase with body size more slowly than does the cell-wall content of the diet. Using the case of the African buffalo, we arrived at calculations which suggest that sufficient intake of a high-fiber diet cannot be maintained to provide the energy necessary to support larger body sizes. Second, with increased body size the very low *MR/GC* ratio allows very long retention times. A point in body size is reached (600–1200 kg) at which retention times are sufficient to achieve relatively complete digestion of the potentially digestible component of forages, regardless of whether the herbivore possesses a selective delay mechanism of the rumen or the "perfect mixing" of the nonruminant model.

Because of the small body size of early ruminants, the evolution of the rumen was probably initiated by selection for the detoxification or synthetic capabilities of foregut fermentation. The foregut then was preadapted for development as a structure for the selective delay of forages when the grasslands expanded.

Changing body size is postulated as a mechanism for differentiating the feeding requirements of herbivores. The fiber composition of plant material is the scaling variable for a resource axis for herbivores. Large herbivores can extract more energy from plant material than can smaller herbivores, but cannot concentrate on the rapidly digestible foods used by small animals because these foods are rare. Therefore, if competition is important in structuring herbivore communities, then body size is probably a factor that contributes to feeding differences.

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APPENDIX

Calculations of the Dry-Season Cell-Wall Content of African Buffalo Diets

FORAGE QUALITY

The digestibility (*%DM*) of leaves, sheaths, and stems was calculated from a regression of % crude protein obtained by Brendon et al. (1963) working with Ugandan cattle and tropical grass. Crude protein values from Sinclair (1977, p. 322, table 34) were used to predict digestibility of the grass parts. For October, digestibility values are estimated as 49.3%, 46.0%, and 43.9% for leaves, sheaths, and stems, respectively. These dry-matter digestibilities appear to be higher than those measured by Stanley-Price (1977). His values were determined on an organic-matter basis, and his procedure is not described or referenced.

The cell-wall content of the leaves, sheaths, and stems at the end of the dry season was estimated at 65%, 77%, and 85%, respectively, from unpublished analysis of dry-season tropical grasses by M. W. Demment.

DIET AND INTAKE

The amount of leaf, sheath, and stem in the diet of a 424-kg buffalo (the average weight of animals sampled in fig. 21 and table 24 of Sinclair's monograph; Sinclair, personal communication) can be calculated.

Digestibility of the diet, as a whole, was calculated by averaging the digestibilities of the grass parts, weighted for their proportion in the diet for October (11% leaves, 39% sheath, 49% stem; Sinclair 1977, fig. 20). The diet's digestibility was estimated as 44.9%.

The total intake of forage (g *DM*/day) for a 424-kg buffalo was calculated by

$$I = \frac{aw^{.75}}{bcd} \tag{A1}$$

where I is the intake (g *DM*/day) and a is a metabolic constant (105 kcal/day). This value is 1.5 × basal metabolism and is used to approximate an animal which is standing most of the day. Taylor et al. (1970) estimate that standing requires 1.7 times basal metabolism. Given the additional costs of locomotion, 1.5 is probably a conservative estimate of a reproductively inactive animal. b is a constant to convert intake from kcal to g *DM* (4.409 kcal/g); c is the proportion of digestible energy not lost to microbial respiration (7.2% lost) or methane production (18% lost; Baldwin et al. 1977); d is the proportion of the intake which is digestible; w is body weight (kg).

Total dietary intake in October for a 424-kg buffalo is 6624.8 g *DM*. This estimate is conservative relative to those made by Sinclair (1977) and is probably the result of higher metabolic requirements and/or lower digestibilities than those used in this calculation.

CELL-WALL CONTENT OF THE DIET

The cell-wall content of the diet for a buffalo greater than 424 kg is calculated as follows. A mass-balance equation (g *DM*) for the buffalo is

$$M_{in} = c\,(D_L B_L + D_{SH} B_{SH} + D_{ST} B_{ST} \tag{A2}$$

$$M_{out} = \frac{aw^{.75}}{bc} \tag{A3}$$

where B is the biomass of the diet (g *DM*) in leaves (L), sheath (SH), and stem (ST); D is the digestibility of leaves (L), sheath (SH), and stem (ST); M is the mass expenditure (*out*) and assimilation (*in*) (g *DM*); both in net energy. Setting M_{in} equal to M_{out} and solving for B_{ST} yields

$$B_{ST} = \frac{1}{D_{ST}}\left(\frac{aw^{.75}}{bc} - D_L B_L - D_{SH} B_{SH}\right). \tag{A4}$$

The amount of cell wall (g *DM*) in this diet is

$$CW_t = C_L B_L + C_{SH} B_{SH} + C_{ST} B_{ST}$$

where CW_t is the cell-wall content of the diet (g *DM*/day); C_L, C_{SH}, and C_{ST} are the cell-wall content (proportion of *DM*) of the leaves, sheath, and stem, respectively. Substituting into eq. (A4) yields

$$CW_t = \frac{C_{ST}}{D_{ST}}\left(\frac{aw^{.75}}{bc} - D_L\,B_L - D_{SH}\,B_{SH}\right) + C_L\,B_L + C_{SH}\,B_{SH}. \tag{A5}$$

Since B_L, B_{SH}, C_L, C_{SH}, D_L, and D_{SH} are all constants (i.e., the assumption that increased costs of body size are met with increased amounts of stem in the diet), the numerical values can be inserted and the equation reduced to the form

$$CW_t = 61.7\,w^{.75} - 539.5. \tag{A6}$$

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